

VEGETATIONAL RESPONSE TO THREE ENVIRONMENTAL GRADIENTS IN THE SALT PLAYA NEAR GOSHEN, UTAH COUNTY, UTAH

Michael G. Skougard¹ and Jack D. Brotherson²

ABSTRACT.— The plant communities and individual plant species in and around a salt playa near Goshen, Utah County, Utah, were studied in relation to gradients for soluble salts, soil moisture, and pH. Forty-eight stands were sampled. Frequency data were taken for all plant species. Soil samples were collected from each site and analyzed to establish the environmental gradients.

Results indicate that the vegetational types respond differentially to the three gradients and can be segregated on the basis of one or more of the gradients. The total soluble salts gradient was found to be the most influential of the three sampled. Correlation analysis indicates that 45 percent of the variation in plant diversity can be accounted for by the three gradients. Distributional patterns of individual plant species are strongly influenced by the three gradients. Niche width measurements exhibited no correlation with the measured gradients.

The study area is at the southern end of Utah Lake, south of Goshen Bay, in Central Utah (Fig. 1). Due to lack of drainage, much of the low-lying land in this area has high concentrations of soluble salts. Depressions in the area accumulate sufficient salt to totally suppress plant growth and become barren playas. Surrounding the playas, zones of vegetation form discrete plant associations with narrow ecotones (Fig. 1). The most salt tolerant or salt dependent types grow closest to the playas. Away from the playa and in the direction of higher ground, the vegetation becomes progressively less salt tolerant.

A general description of the climate near Goshen is given by Hansen (1974). Temperatures were shown to gradually increase through May and June, with July having an average daily high of 34 C. Daily mean relative humidity was lowest from mid-July through mid-August. Relative humidity (except for six evenings) reached 100 percent every night during the growing season. Growing season precipitation was confined to two seasons, the first in late May through early June and the second in late August through early September.

Based upon growth ring analysis of the woody stems of *Allenrolfea occidentalis*, Hansen and Weber (1975) concluded that the study area has become more moist in the last 35 years. They attributed this change in soil

moisture to increased surface and subsurface water from irrigation of nearby fields.

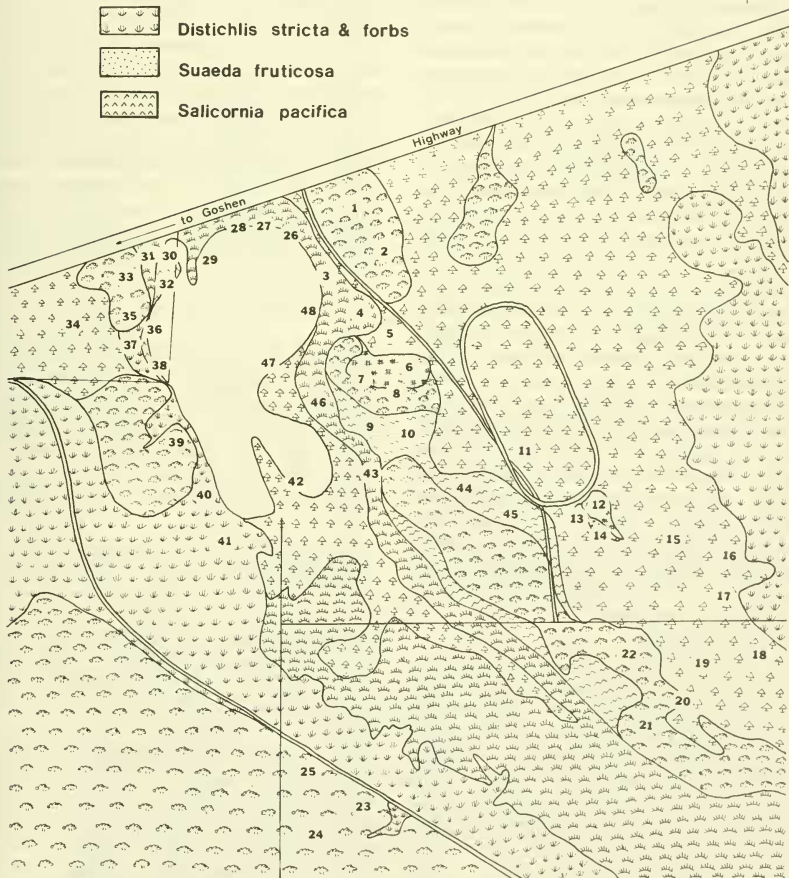
The effect of saline and alkali substrates on plants has been studied by several authors. Magistad (1945) reviewed over 350 papers dealing with plant growth on saline and alkali soils. Waisel (1972) outlined some of the major problems facing plants growing in hydromorphous salt playas. In his discussion, Waisel recognized high salinity, low partial pressure of oxygen, high carbon dioxide concentrations, and altered oxidation-reduction relations as major problems. Magistad (1945) differentiated between the effects of saline and alkali soils on plant growth. Saline soils reduced plant growth by increasing osmotic potential of the soil solution. On alkali soils, however, plant growth was affected by reduced soil permeability, lack of oxygen, malnutrition, chlorosis, and even corrosive action.

In arid regions the most crucial factor limiting plant growth is available water, and salinity is considered the second most limiting variable (Chapman 1966). The largest area of salt-affected soils combine both adverse features—salinity and aridity. Plants native to such areas combine adaptations which ameliorate the effects of osmotic withdrawal of water and sodium (and other ion) toxicity (Dregne 1963). The most important factor affecting plant distribution in saline soils is the

¹Department of the Army, Corps of Engineers, Regulatory Assessment Section, P.O. Box 60267, New Orleans, Louisiana 70160.

²Department of Botany and Range Science, Brigham Young University, Provo, Utah 84602.

-  Playa & *Salicornia rubra*
-  *Sarcobatus vermiculatus*
-  *Allenrolfea occidentalis*
-  *Distichlis stricta*
-  *Atriplex confertifolia*
-  *Atriplex tridentata*
-  *Distichlis stricta* & forbs
-  *Suaeda fruticosa*
-  *Salicornia pacifica*



g. 1. Vegetation map of the study area illustrating vegetation distribution patterns and location of study plots.

osmotic concentration of the soil solution (Ungar, Hogan, and McClelland 1969, Waisel 1972, Al-Jibury 1972).

Chapman (1966) indicated that the zonation patterns of plant communities growing around saline areas were related to soil salinity. The salinity was expressed by the amount of sodium chloride or soluble chloride present in the soil or in terms of osmotic pressures.

The effects of hydrogen ion concentration on plants are not well known, but include alterations in nutrient availability and/or toxicity (Kramer 1956) and disease susceptibility (Daubenmire 1959). The availability of manganese, iron, copper, molybdenum, and zinc in a soil tends to decline as pH values rise above 7.0 (Buckman and Brady 1969). In regard to plant distribution, Olsen (1924) concluded that soil hydrogen ion concentration affected plant cover. This was, however, refuted by Daubenmire (1959), who stated that pH was not as closely correlated with biological phenomenon as formerly believed. Ungar, Hogan, and McClelland (1969) found that the range of hydrogen ion concentration tolerated by plant communities and species was broad. Their findings indicate that hydrogen ion concentration was probably not one of the environmental factors exerting a strong influence on species distribution.

Studies concerning indicator significance of desert shrubs have been conducted by a number of authors. In a study of plant distribution in the Escalante Desert of Utah, Lambert (1940) found a definite correlation between soil alkalinity and plants found growing under various conditions of alkalinity. Harris (1920) compiled a list of indicator plants and described the soil conditions they indicated.

In a study of the indicator significance of some shrubs in the Escalante Desert of Utah, Fireman and Hayward (1952) described the distribution of *Sarcobatus vermiculatus*, *Atriplex confertifolia*, and *Artemisia tridentata* stands in relationship to soil pH and exchangeable sodium. They found that the distribution of these plants was correlated with the pH and exchangeable sodium concentration of the soil.

Fautin (1946), in a study of the northern desert shrub biome in Utah, outlined the gen-

eral soil and moisture requirements of a number of the plant species involved. Gates, Stoddart, and Cook (1956) found local soil variations insufficient to explain the distribution of the different plant communities on the salt desert of Utah. Goodman (1973) and Goodman and Caldwell (1971) attempted to explain mosaic patterns of dominant salt desert plant communities and their subdominants on the basis of ecotypic variation rather than on the basis of soil chemistry.

In a study of the flora of the Great Salt Lake region of Utah, Flowers and Evans (1965) described the vegetation of the saline and nonsaline areas around Great Salt Lake. They found the vegetation in distinct patterns around the salt playas. They attributed the patterns to increasing salt concentrations toward the center of the playas. The following sequence was determined for plant invasion of playas (plants are listed in order of decreasing tolerance to soil salinity): 1) *Salicornia rubra* or *Salicornia pacifica*, 2) *Suaeda erecta*, 3) *Allenrolfea occidentalis*, 4) *Distichlis spicata*, and 5) *Suaeda fruticosa*.

METHODS AND MATERIALS

Forty-eight 10 × 10 m study plots of homogenous vegetation were sampled within the major vegetation zones. Eight meter-square quadrats were located at random within each study plot, and species frequency data were taken. Quadrat frequency was computed for all species in each plot (Phillips 1959).

A Constancy times Frequency (C × F) Index (Anderson 1964, Curtis 1959) was computed for all plant species in the study (Table 1). This index gives an indication of the relative importance of each species in the community. For instance, *Salicornia rubra*, with a C × F Index of 2278 would be the most widespread species in the study area (Table 1).

Soil samples were collected during the third week of August. This was considered the time when soil moisture values would exhibit maximum differential between the driest and the most moist habitats (Hansen 1975). This differential was enhanced by the fact that there had not been any precipitation in the area for three weeks preceding

the collection of data. Soils were collected only once during the growing season, since only the relative magnitude between community differences for the various soil parameters was required for our purposes.

The soil samples were collected from two soil pits dug at each study plot. Samples were taken from the surface inch, 6- to 12-inch

level, and the 18-inch level. Samples were analyzed in the laboratory for total soluble salts, hydrogen ion concentration, and percent soil moisture. Total soluble salts were determined by means of a Beckman model RC216B2 conductivity bridge. Hydrogen ion concentration was determined using a glass electrode Sargent-Welch pH meter. Percent soil moisture was determined by weighing fresh soil samples, drying for 48 hours at 110 C, and then reweighing.

Soil data from the three depth horizons and the two pits per site were averaged (to obtain values used in the establishment of the environmental gradients for total soluble salts, hydrogen ion concentration (to obtain a workable gradient for hydrogen ion concentration, pH values were carried out to hundredth of a pH unit), and percent soil moisture (Beadle, Whalley, and Gibson 1957). Stands common to a portion of the gradient were combined for analytical purposes, and average frequency values for participating species within each group were computed (Table 2).

After stands common to a portion of the gradient were combined, the response of individual species and of combinations of species of common growth form (i.e., shrubs, grasses, annuals, species with succulent stems, forbs, and perennials) were graphed (using frequency data as the criterion of performance) against the environmental gradient to display distribution trends (Figs. 2-4). Average percent frequency values for all plant species were computed for all plots assigned to each segment of the gradient. Average values based upon all plots common to a given segment of the gradient shows smoother

TABLE 1. Species listed in order of decreasing constancy times frequency (C × F) index numbers

Species	C × F Index	Percent constancy	Average frequency
<i>Salicornia rubra</i>	2278	54	42.2
<i>Distichlis spicata</i>	1250	50	25.0
<i>Lepidium perfoliatum</i>	1154	38	30.4
<i>Allenrolfea occidentalis</i>	1100	44	25.0
<i>Bromus tectorum</i>	842	33	25.5
<i>Suaeda fruticosa</i>	460	31	14.8
<i>Sarcobatus vermiculatus</i>	288	23	12.5
<i>Atriplex confertifolia</i>	218	21	10.4
<i>Salicornia pacifica</i>	202	21	9.6
<i>Kochia americana</i>	137	21	6.5
<i>Atriplex tridentata</i>	125	13	9.6
<i>Triglochin maritima</i>	113	16	7.0
<i>Sueda depressa</i>	57	13	4.4
<i>Cordylanthus canescens</i>	26	10	2.6
<i>Descurainia sophia</i>	23	6	3.9
<i>Poa nevadensis</i>	20	8	2.6
<i>Haplopappus lanceolatus</i>	20	8	2.6
<i>Chenopodium album</i>	20	8	2.3
<i>Puccinellia airoides</i>	13	8	1.6
<i>Atriplex patula</i>	10	8	1.0
<i>Sitanion hystrix</i>	7	6	1.2
<i>Opuntia polyacantha</i>	7	6	1.2
<i>Chrysothamnus nauseosus</i>	3	4	.8
<i>Agropyron smithii</i>	3	2	1.3
<i>Poa sandbergii</i>	2	4	.5
<i>Sporobolus airoides</i>	2	4	.5
<i>Salsola iberica</i>	2	2	.8
<i>Camelina microcarpa</i>	2	4	.5
<i>Artemisia tridentata</i>	1	2	.3

TABLE 2. Characteristics of the study sites included in each segment of the soluble salts, soil moisture, and pH gradients.

Groups	Total soluble salts in p.p.m.			Soil moisture as percent of dry weight			Hydrogen ion concentration (pH)		
	Lower boundary	Upper boundary	Mean*	Lower boundary	Upper boundary	Mean*	Lower boundary	Upper boundary	Mean*
1	636	879	732	3.1	10.2	8.0	8.17	8.27	8.22
2	934	1,686	1,263	10.5	13.4	12.3	8.32	8.43	8.38
3	3,266	4,901	4,176	15.0	18.0	16.5	8.47	8.54	8.51
4	9,522	13,152	11,159	18.6	19.9	19.2	8.55	8.59	8.56
5	14,906	19,096	16,577	20.5	22.4	21.2	8.62	8.70	8.67
6	22,819	22,152	24,090	23.1	26.5	24.6	8.79	8.88	8.83
7	26,008	27,037	26,543	27.5	32.0	29.7	9.03	9.04	9.03

*Mean is an expression of the average values for all stands included in the group.

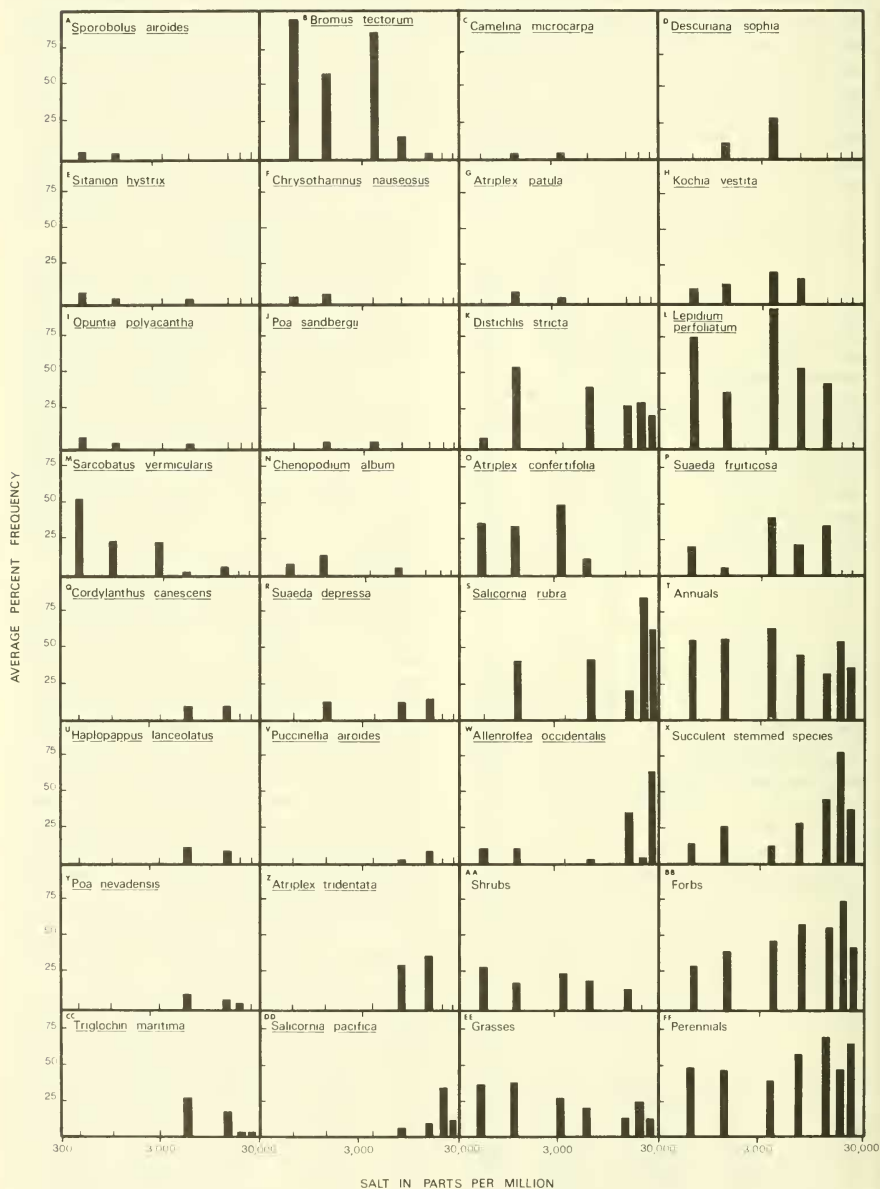


Fig. 2. Individual plant species and growth form response to soil soluble salts concentration in the soil.

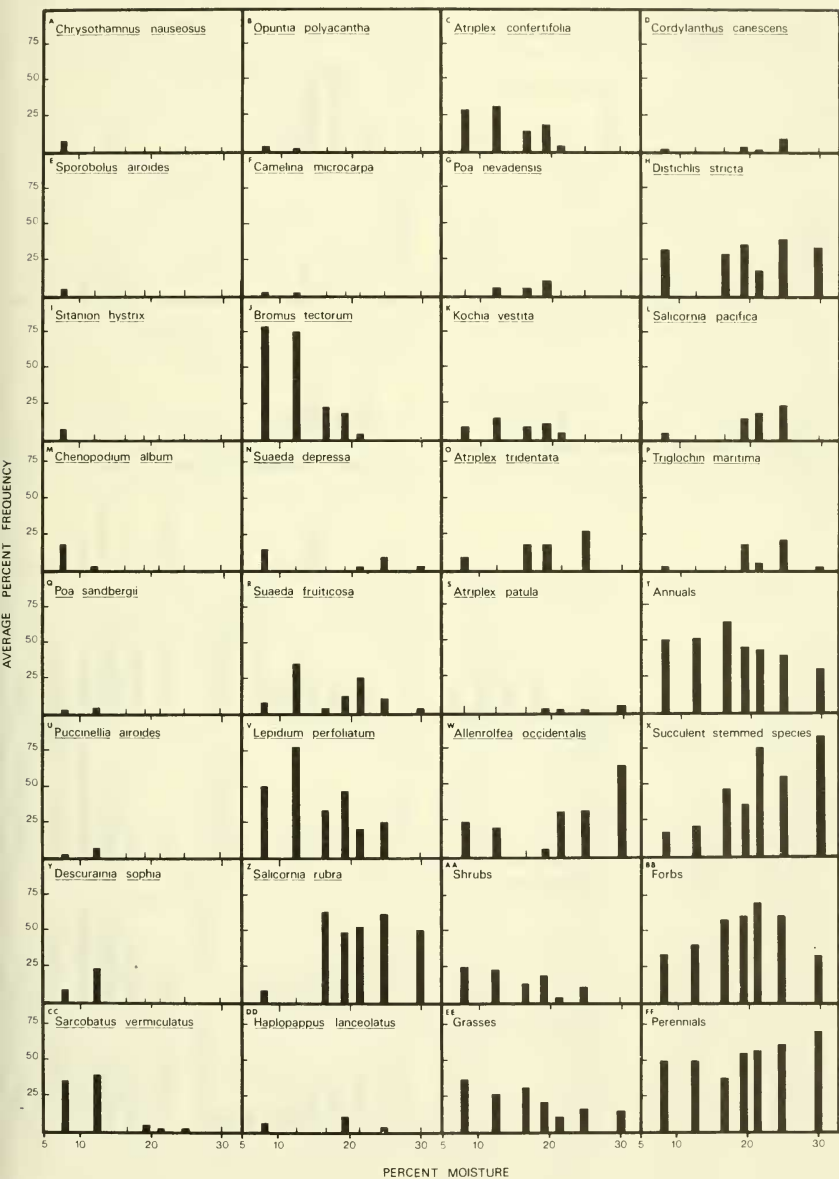


Fig. 3. Response of individual plant species and growth form response to the soil moisture.

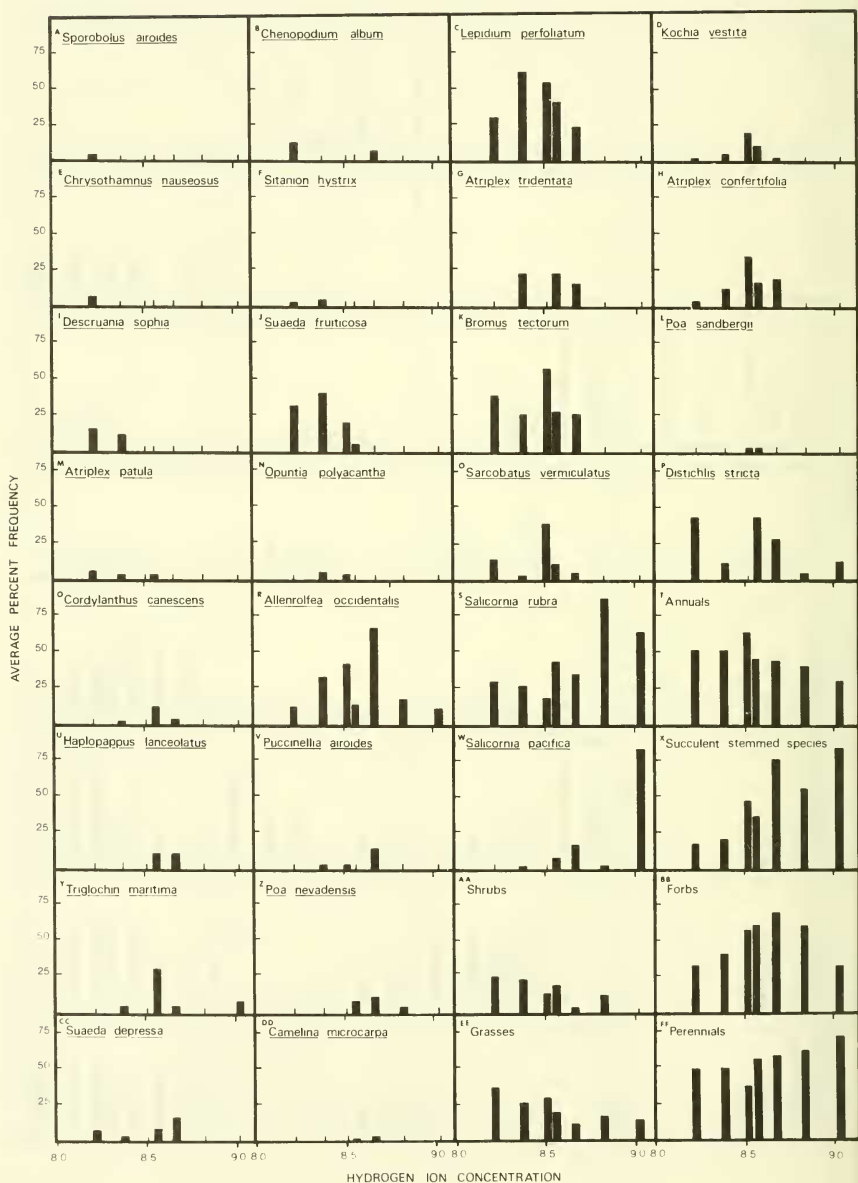


Fig. 4. Response of individual plant species and growth forms to soil pH.

trends along the gradient for any variable than do individual values for that variable at each plot (Bross 1974).

Stand diversity and species niche width values were computed from frequency data using the equation:

$$B = \frac{1}{\sum pi^2}$$

where "B" is equal to either the species niche width or stand diversity, and "pi" is a measure of the relative abundance of a species in a given habitat (Levins 1966, MacArthur 1972). Species niche width values were obtained by summing "pi" values across all stands. Stand diversity values were obtained by summing "pi" values for all species found within a given stand.

Total soluble salts, hydrogen ion concentration, and percent soil moisture preference indices (Table 3) were computed for all participating species by the following equation:

$$\text{Preference Index} = \frac{\text{Frequency of species A times the gradient value of the stand in which it occurs}}{\text{Frequency values of species A across all stands in which it occurs}}$$

This was done in an attempt to facilitate comparison of species niche width values and their general distribution patterns along the total soluble salts, hydrogen ion concentration, and percent soil moisture gradients.

Correlation analyses (Hall 1971, Dick 1971) were conducted to determine the degree to which the different gradients were associated, and the degree to which species niche width value and stand diversity indices were controlled and/or affected by the measured gradient factors (Tables 4 and 5). Multiple regression analysis (Snedecor and Coch-

TABLE 3. Species niche width (N.W.), salt preference (S.P.), hydrogen ion concentration preference (H.P.), and moisture preference (M.P.) index numbers, in order of niche width.

Species	N.W.	S.P.	M.P.	H.P.
<i>Agropyron smithii</i>	1.00	639.00	3.11	8.19
<i>Artemisia tridentata</i>	1.00	639.00	3.11	8.19
<i>Salsola iberica</i>	1.00	639.00	3.11	8.19
<i>Chrysothamnus nauseosus</i>	1.82	835.67	4.04	8.22
<i>Camelina microcarpa</i>	2.00	2,711.65	11.16	8.63
<i>Poa sandbergii</i>	2.00	3,029.00	11.38	8.53
<i>Sporobolus airoides</i>	2.00	786.50	3.81	8.22
<i>Chenopodium album</i>	2.64	4,441.44	5.57	8.32
<i>Opuntia polyacantha</i>	2.70	3,614.25	13.26	8.41
<i>Sitanion hystrix</i>	2.70	3,960.90	11.89	8.46
<i>Descurainia sophia</i>	2.77	3,053.75	10.81	8.29
<i>Haplopappus lanceolatus</i>	2.80	12,447.90	17.57	8.60
<i>Poa nevadensis</i>	2.95	15,183.80	16.79	8.65
<i>Puccinellia airoides</i>	3.04	18,200.17	15.81	8.57
<i>Atriplex patula</i>	3.62	5,539.30	24.13	8.34
<i>Atriplex tridentata</i>	4.60	16,711.27	20.44	8.49
<i>Triglochin maritima</i>	4.72	14,185.63	22.47	8.59
<i>Cordylanthus canescens</i>	4.82	13,438.70	22.23	8.56
<i>Suaeda depressa</i>	5.06	12,196.93	17.96	8.52
<i>suaeda fruticosa</i>	5.83	9,542.13	18.09	8.47
<i>Salicornia pacifica</i>	7.42	23,015.97	21.46	8.90
<i>Kochia americana</i>	7.75	7,348.80	15.69	8.51
<i>Atriplex confertifolia</i>	8.53	3,339.07	13.75	8.51
<i>Bromus tectorum</i>	13.83	3,954.18	12.08	8.45
<i>Allenrolfea occidentalis</i>	14.93	22,558.37	21.49	8.55
<i>Lepidium perfoliatum</i>	17.48	6,646.18	15.14	8.44
<i>Distichlis spicata</i>	21.40	14,827.39	20.05	8.58
<i>Salicornia rubra</i>	23.13	20,393.93	21.79	8.90
<i>Sarcobatus vermiculatus</i>	29.76	3,126.67	10.59	8.46

ran 1967) was conducted to determine the combined influence of pH, salinity, and soil moisture on stand diversity and species niche width.

RESULTS AND DISCUSSION

The response of the plant communities to the soluble salts gradient was generally clear-cut. All community types segregate along the gradient: however, the most clearly defined segregations occurred among those stands dominated by halophytic species.

With the exception of stand 34 (Fig. 1), which exhibited 13,095 ppm total soluble salts, all of the stands of *Allenrolfea occidentalis* exhibited total soluble salts concentrations between 26,401 and 27,037 ppm. Stands dominated by *Salicornia rubra* were found to occur from 22,819 ppm total soluble salts to 26,909 ppm. *Salicornia rubra* also occurred as

a subdominant in the *Distichlis spicata* stands which exhibited salt concentrations of around 10,468 ppm. The stands of *Salicornia pacifica* were found to occur in soils with 24,265 to 26,407 ppm total soluble salts.

Along the lower end of the salt gradient there was less obvious order. A great deal of overlap occurred between the plant communities on that portion of the gradient. *Sarcobatus-Atriplex* stands exhibited ranges of from 635 to 11,226 ppm total soluble salts. Stands of *Atriplex confertifolia* were found on plots having from 772 to 4,900 ppm salts. Stands dominated by *Suaeda fruticosa* were found in soils where salt concentrations ranged from 3,266 to 15,619 ppm. *Atriplex tridentata* stands occurred in soils which exhibited total soluble salts concentrations ranging from 9,255 to 18,506 ppm.

Distichlis spicata communities tended to be the least restricted of any of the communities found along the gradient. Stands of *Distichlis spicata* exhibited ranges in soluble salt concentration of 1,211 to 26,533 ppm.

In comparison to the total soluble salts gradient, the soil moisture gradient produced maximum segregation of plant species at lower moisture levels. Stands of *Sarcobatus vermiculatus* and *Atriplex confertifolia*, both in pure stands and in association with each other, were found primarily at the low moisture end of the gradient. With the exception of one stand, all communities of *Sarcobatus vermiculatus* and its codominants were found in soils with less than 12 percent soil moisture. *Atriplex confertifolia* stands occurred in soils showing between 10 and 19 percent moisture. Stands of *Suaeda fruticosa* were found along the moisture gradient in soils having 12 to 21 percent moisture. *Allenrolfea occidentalis* stands occurred in soils having between 10 and 31 percent moisture. *Salicornia rubra* communities were found to occupy the middle portions of the moisture gradient and occurred in soils which exhibited a range of 15 to 20 percent moisture. *Salicornia pacifica* stands occurred next to *Salicornia rubra* stands on the soil moisture gradient and occupied areas exhibiting 18 to 23 percent soil moisture.

The hydrogen ion concentration (pH) gradient, like the salt and moisture gradients, affected some community types more than

TABLE 4. Correlation of environmental gradients with each other and with the plot diversity indices. Given are "r" and "r'" values and levels of significance (n = 48). Multiple regression analysis of all three environmental gradients versus diversity index values results in "R" = .45.

Variables correlated	"r"	"r'"	Significance level
Salt-moisture	.3811	.15	.01
Salt-pH	.1080	.01	N.S.
Moisture-pH	-.7813	.61	.01
Salt-diversity index	-.6068	.37	.01
Moisture-diversity index	-.3766	.14	.01
pH-diversity index	-.0113	.0001	N.S.

TABLE 5. Correlation of species preference indices for three variables with each other or with niche width values. Given are "r" and "r'" values and levels of significance (n = 29). Multiple regression analysis of all three preference indices versus niche width results in "R" = .11.

Variables correlated	"r"	"r'"	Significance level
Salt-Moisture	.2509	.06	N.S.
Salt-pH	.4134	.17	.05
Moisture-pH	-.6829	.47	.01
Salt-N.W.	.2756	.08	N.S.
Moisture-N.W.	.0526	.003	N.S.
pH-N.W.	.2025	.04	N.S.

others. Stands dominated by either *Salicornia rubra* or *Salicornia pacifica* were those most strictly segregated along the hydrogen ion concentration gradient. *Salicornia rubra* dominated stands were all found between pH values of 8.79 and 8.88. As a co-dominant with *Distichlis spicata*, however, *Salicornia rubra* grew in soils exhibiting a pH of 8.41. The plant communities occurring in soils with a mean pH of 9.0 or greater were all dominated by *Salicornia pacifica*. The stands dominated solely by the two species of *Salicornia* were found to exhibit the narrowest pH ranges of all stands studied.

Other stands exhibited much broader pH ranges. Stands of *Suaeda fruticosa*, for example, were found to occupy areas with pH values between 8.17 and 8.35 mean soil pH. There were no stands dominated solely by *Sarcobatus vermiculatus* included in this study. It was always found growing with co-dominates (i.e., *Agropyron smithii*, *Chrysothamnus nauseosus*, and *Atriplex confertifolia*). *Atriplex tridentata* stands occurred in areas where mean pH values ranged from 8.34 to 8.59. *Allenrolfea occidentalis* stands exhibited variations in mean pH values of 8.42 to 8.69.

Distichlis spicata communities again exhibited wide tolerance ranges for gradient values (i.e., pH levels from 8.24 to 8.59) and thus seemed to be the least restricted by hydrogen ion concentrations in the soil of the communities studied.

The results of correlation and multiple regression analyses between gradients are found in Table 4. The salt and moisture gradients correlated at a significance level of .01 with an "R" of 0.61. Diversity Index values correlated with salt at the .01 level of significance and an "R" of .37, with moisture also at the .01 level of significance with an "R" of .14; and with hydrogen ion concentration the correlation was nonsignificant. The multiple regression analysis of Diversity Indices and all three gradients yielded an "R" value of .45.

The response of individual plant species and selected plant growth forms to the three gradients were studied by plotting the average percent frequency of each species or vegetation type against each of the three

gradients. Figures 2 through 4 represent the results.

Figure 2 shows the response of individual plant species to total soluble salts. *Sporobolus airoides*, *Sitanion hystrix*, *Opuntia polyacantha*, *Chrysothamnus nauseosus*, and *Bromus tectorum* can be classified as having low tolerance to salt. Species which exhibited their greatest frequencies between 934 and 13,152 ppm total soluble salts were classified as moderately tolerant. These species included *Poa sandbergii*, *Chenopodium album*, *Camelina microcarpa*, *Atriplex patula*, *Distichlis spicata*, *Atriplex confertifolia*, *Sarcobatus vermiculatus*, *Descurainia sophia*, *Kochia americana*, and *Lepidium perfoliatum*. Tolerant species were those which exhibited their greatest frequencies on sites having between 14,906 and 25,152 ppm total soluble salts. Included in this classification were *Suaeda fruticosa*, *Cordylanthus canescens*, *Haplopappus lanceolatus*, *Poa nevadensis*, *Triglochin maritima*, *Suaeda depressa*, *Puccinellia airoides*, *Atriplex tridentata* and *Salicornia pacifica*. Species which exhibited their greatest frequencies in soils with salt concentrations in excess of 26,008 ppm were classified as highly tolerant. *Allenrolfea occidentalis* and *Salicornia rubra* were classified in this group. Only the extremely high salt concentrations of the playa were limiting to these two species, which tolerated conditions on the edge of the playas. This response of various plant growth forms to the salt gradient are shown in Figure 2. Shrubs and grasses decreased as total soluble salts increased. Forbs increased with total soluble salt up to about 25,152 ppm and then decreased. Perennials increased slightly as total soluble salts increased. Succulent stemmed species increased rapidly at higher total soluble salts concentrations. Annuals exhibited little response to the salt gradient.

Individual plant species response to soil moisture is shown in Figure 3. *Chrysothamnus nauseosus*, *Sporobolus airoides*, and *Sitanion hystrix* were restricted to the most xeric portions of the soil moisture gradient. *Opuntia polyacantha*, *Camelina microcarpa*, *Puccinellia airoides*, *Poa sandbergii*, and *Descurainia sophia* were generally restricted to areas from 3 to 13 percent soil moisture, although *Opuntia polyacantha* did appear at a

very low average frequency between 20 and 22 percent soil moisture. *Sarcobatus vermiculatus* and *Atriplex confertifolia* were most frequent from 3 to 13 percent soil moisture, but *Sarcobatus vermiculatus* was found in soils having up to 26 percent moisture and *Atriplex confertifolia* in soils having up to 22 percent moisture. The range of *Salicornia rubra* along the soil moisture gradient was from 3 to 32 percent. However, it exhibited very high average frequency from 15 to 31 percent soil moisture. *Poa nevadensis* was restricted along the soil moisture gradient to soils with 11 to 20 percent moisture content. *Atriplex tridentata* increased in average frequency as soil moisture increased from 3 to 25 percent moisture. *Kochia americana* was restricted to areas of less than 22 percent soil moisture. *Salicornia pacifica* and *Trilochin maritima* exhibited their greatest average frequencies from 19 to 26 percent soil moisture. *Salicornia pacifica* was found from 3 to 26 percent soil moisture and *Trilochin maritima* was found in soils with 3 to 31 percent soil moisture. *Atriplex patula* was restricted to soils exhibiting from 19 to 32 percent moisture and was most frequent in the more mesic portions of the gradient. *Allenrolfea occidentalis* occurred all along the soil moisture gradient from 3 to 32 percent, but was most successful in the more mesic soils.

Several species exhibited little response to the soil moisture gradient. *Suaeda depressa* occurred along the gradient in soils which exhibited from 3 to 31 percent and did not exhibit any area of optimum response. *Suaeda fruticosa* had a range of soil moisture from 3 to 32 percent. *Haplopappus lanceolatus* and *Cordalanthus canescens* were found in soils exhibiting 3 to 26 percent moisture. As with the total soluble salts gradient, *Distichlis spicata* was found most ubiquitously across the soil moisture gradient, from 3 to 32 percent moisture.

The plant growth forms responded to moisture with essentially the same patterns as they displayed for total soluble salts. Shrubs, grasses, and annuals all declined in average frequency as moisture increased. Succulent stemmed species increased rapidly with increasing soil moisture. Forbs increased to a point near the most mesic end of the gradient and then declined rather rapidly. Perennials

increased somewhat with increasing soil moisture.

The responses of the individual plant species to the hydrogen ion concentration gradient are shown in Figure 4. Species were classified as being of low, moderately tolerant, tolerant, and highly tolerant in response to soil alkalinity. Species which exhibited low tolerance to increasing alkalinity in the soil were *Sporobolus airoides*, *Chrysothamnus nauseosus*, *Descurainia sophia*, *Atriplex patula* and *Sitanion hystrix*. Moderately tolerant species were those with their greatest average frequencies between pH 8.17 and 8.54. These species were *Suaeda fruticosa*, *Opuntia polyacantha*, *Lepidium perfoliatum*, *Atriplex tridentata*, *Bromus tectorum*, *Sarcobatus vermiculatus*, *Kochia americana*, *Atriplex confertifolia*, and *Poa sandbergii*. Species which exhibited their greatest average frequencies along the hydrogen ion concentration gradient between 8.55 and 8.88 were tolerant species. Species classified as tolerant were *Distichlis spicata*, *Cordylanthus canescens*, *Haplopappus lanceolatus*, *Trilochin maritima*, *Suaeda depressa*, *Allenrolfea occidentalis*, *Puccinellia airoides*, *Poa nevadensis*, and *Camelina microcarpa*. Highly tolerant species were *Salicornia rubra* and *Salicornia pacifica*, which exhibited their greatest average frequencies in soils with pH values over 9.00.

The plant growth form responses to the hydrogen ion concentration gradient can also be observed in Figure 4. Shrubs responded to hydrogen ion concentration along a modified "bell-shaped" curve. That is, the average frequencies of the shrubs were greatest in the middle of the gradient and tapered downward toward either end of the gradient. Grasses and annuals exhibited little response to the alkalinity gradient. Succulent stemmed species responded to the hydrogen ion concentration gradient in a manner very similar to their responses to the salt and moisture gradients. That is, they increased at an accelerating rate across the gradient. Forbs exhibited a "U-shaped" response to increasing pH values. Perennials, like succulent stemmed species, responded to the hydrogen ion concentration gradient in a manner similar to their response to salts and soil moisture.

Table 5 contains the results of the correla-

tion analysis between niche width values and the preference index values of the plant species studied. Niche width was not significantly correlated to any of the three species preference indices. There was a nonsignificant correlation between salt and moisture preference values. Salt and hydrogen ion concentration correlated at the 0.05 level of significance with an "R²" of .17. Moisture and hydrogen ion concentration were negatively correlated at the 0.01 level of significance with an "R²" of .47. The multiple regression analysis of niche widths and species preference indices was nonsignificant.

The Goshen salt playa is typical of a great number of small playas found in the area south of Utah Lake. The vegetation surrounding the playa ranges from halophytes immediately surrounding the playa to non-halophytes (glycophytes) on the small knolls adjacent to the playa. Transition zones between the various plant communities were characteristically sharp; plant communities nearest the playa exhibited the narrowest ecotones. The plant species responded to various environmental gradients and tended to sort themselves into discreet plant communities. The sharp zonation patterns were also noted by Flowers and Evans (1965). They attributed the narrow ecotones to the increasing gradient of salt concentration toward the center of the playa.

Table 1 is a species list with the species arranged in order of decreasing Constancy times Frequency (C × F) Index values. The C × F Index is used as a measure of the relative importance of a particular species across the entire system of communities. Those species exhibiting higher C × F Index values were, in this study, generally the most salt tolerant (i.e., *Salicornia rubra* *Distichlis spicata*, *Allenrolfea occidentalis*). The effects of cattle grazing and other disturbance on the area were evidenced by the relative importance of two introduced species, *Lepidium perfoliatum* and *Bromus tectorum*.

Of the three environmental factors studied, total soluble salts appeared to be the most important factor regulating the distribution patterns of the various plant communities studied. Although each of the factors studied exhibited an effect on some or all of the communities sampled, total soluble salts were the

most restrictive, particularly at high concentrations. Moisture seemed to exhibit the least effect upon the segregation of the various communities, as there was little order and a great deal of overlapping of the moisture values of the stands studied. The hydrogen ion concentration of the soil was quite restrictive to some of the communities. For instance, stands of *Salicornia rubra* and *Salicornia pacifica* were all restricted to sites having high pH levels. Because both of these species occurred as co-dominants with other species in communities exhibiting lower levels of hydrogen ion concentration, it was felt that areas dominated by these species are habitat types not environmentally suitable to other plants, which at lower pH ranges tended to out-compete the *Salicornia* species. It might also be that, where these two species are found within other vegetation types, micro-habitat relationships may well echo the habitats they dominate.

The three gradients did not exhibit particularly close correlation (Table 4). The general lack of high degrees of correlation between the three gradients indicates that the gradients functioned somewhat independently of one another. The correlation coefficients, significance levels and "R²" values indicate that soluble salts and moisture gradients influenced most strongly the species diversity in the plant communities considered in this study. Hydrogen ion concentration, however, exerted little or no influence on the diversity of the stands sampled.

A multiple regression analysis of the three environmental factors versus the diversity index yielded an "R²" value of .45. This would indicate that about 45 percent of the diversity exhibited by the stands studied can be accounted for by variation in total soluble salts, soil moisture, and hydrogen ion concentration in the soil. The variation that remains unaccounted for must be looked for in other factors, such as the impact of disturbance by man and his agents (i.e., livestock), specific ions in the soil, soil texture, experimental error, or other unmeasured factors.

Almost all of the species studied exhibited distinctive distribution patterns in relation to the total soluble salts gradient, as did some of the vegetative growth forms (i.e., shrubs,

grasses, succulent stemmed species, forbs, and perennials). This would indicate that the salt gradient was important as an environmental factor in determining the distribution patterns of the individual plant species growing around the Goshen salt playa. This fact concurs with the findings of a number of earlier authors (Lambert 1940, Harris 1920, Fautin 1946, Fireman and Hayward 1952, Al-Jibury 1972).

Sarcobatus vermiculatus (Fig. 2M) was most frequent around the Goshen salt playa in salt concentrations ranging from 635 to 4,901 ppm. This range corresponds to the findings of various earlier authors who stated that *S. vermiculatus* was indicative of 3,600 ppm (Harris 1920) and 4,000 ppm soluble salt (Lambert 1940). Fireman and Hayward (1952) found *S. vermiculatus* indicative of higher salt concentrations in the soil than were indicated by *Atriplex confertifolia*. This does not agree with the findings of our study. Although the basic ranges of total soluble salts in the soil were similar for *Sarcobatus vermiculatus* and *Atriplex confertifolia*, the frequency of *Atriplex confertifolia* (Fig. 2o) tended to increase with increasing salts and *Sarcobatus vermiculatus* tended to decrease in frequency.

The most salt tolerant plant species which grew around the Goshen salt playa were *Salicornia pacifica*, *Salicornia rubra*, and *Allenrolfea occidentalis*, according to salt preference index numbers (Table 5). This basic conclusion is corroborated by other studies (Flowers and Evans 1965, Fautin 1946, Harris 1920). Ungar, Hogan, and McClelland (1969) found that *Salicornia rubra* grew in wet saline soils, but did best in areas of reduced salinity. This conclusion conflicts somewhat with the findings of this study. Evidence was felt to be supportive of the hypotheses of Ungar (1966) and Barbour (1970). They stated that they believed there are few, if any, obligate halophytes, but halophytes grew in highly saline areas because they did not compete well in nonsaline environments, whereas species which grow well in nonsaline areas cannot withstand high levels of salinity, thus leaving these highly saline habitats open to "halophyte" colonization.

Distichlis spicata was not particularly regulated by total soluble salts in this study.

This species was also found to be ubiquitous in saline areas near Lincoln, Nebraska (Ungar, Hogan, and McClelland 1969). *Distichlis spicata*, in this study, exhibited little evidence of being regulated strongly by any of the three gradient factors studied. However, it did tend to decrease in average frequency at higher pH values.

Sarcobatus vermiculatus was most frequent in soils where the upper 18 inches exhibited 3 to 13 percent moisture. This is in general agreement with the findings of Flowers and Evans (1965). They noted that *S. vermiculatus* grew in soils with 5.9 to 6.2 percent moisture at 30 cm depth. These findings would seem to conflict with the study by Fautin (1946), in which he stated that *S. vermiculatus* required large amounts of water. However, *S. vermiculatus* is a species which has rather long taproots and therefore the moisture content of the more shallow layers of soil would not necessarily be indicative of this species' true moisture requirements.

Allenrolfea occidentalis, *Salicornia rubra*, *Salicornia pacifica*, and *Distichlis spicata* all exhibit moisture preference values in excess of 20 percent (Table 3). These results generally concurred with results of other studies for the same species (Flowers and Evans 1965, Ungar, Hogan, and McClelland 1969, Hansen 1975). Although these species grew best in very moist soils, as indicated by their moisture preference values, three of them had wide ranges along the moisture gradient. *Distichlis spicata*, as was mentioned earlier, exhibited little effect by soil moisture and ranged across the moisture gradient in a manner which would indicate that the moisture levels encountered by this and a number of other species at the Goshen salt playa are not limiting. The fact that the three species just mentioned exhibited such wide ranges across the moisture gradient and yet were so limited in their habitats (with the exception of *Distichlis spicata*) tends to support the hypothesis that it was competition from other species which was limiting their distribution.

Very definite responses to the hydrogen ion concentration gradient can be observed for a large number of the plant species involved in this study. Although there was a significant correlation between the soil moisture and hydrogen ion concentration

gradients (Table 4), there also existed sufficiently different responses by several species (i.e., *Distichlis spicata*, *Salicornia pacifica*, *Allenrolfea occidentalis*, *Triglochin maritima*, *Sarcobatus vermiculatus*, *Bromus tectorum*, etc.) to indicate that hydrogen ion concentration influenced the distribution patterns of the plant species around the Goshen salt playa.

In their study of *Salicornia pacifica*, Hansen and Weber (1975) stated that *Salicornia pacifica* was found in the soils with pH values of 7.7, and that *Distichlis spicata* tolerated higher hydrogen ion concentrations than *Salicornia pacifica*. In this study, *Salicornia pacifica* was found to be almost completely restricted to soils with pH values in excess of 9.0, but *Distichlis spicata* became less frequent when soil pH values exceeded 8.70. Hansen and Weber also stated that *Distichlis spicata* may survive in soils with pH values between 8.0 and 9.0. The results of this study support the supposition of Hansen and Weber regarding the pH range of *Distichlis spicata*.

Quigley (1956) found that *Allenrolfea occidentalis* consistently occurred in soils of pH 8.0 and above. Flower and Evans (1965) indicated in their results that *A. occidentalis* was found in soils of about pH 8.4. The results of these two studies concur with the findings of our study, which indicate that *A. occidentalis* was most frequent between pH 8.32 and 8.70.

Sarcobatus vermiculatus (Fig. 4) was found to be most frequent in soils with pH values of about 8.50. Flower and Evans' (1965) results indicate that *S. vermiculatus* grew in soils with pH values of 8.6 to 9.6. Fireman and Hayward found that *S. vermiculatus* grew in soils with higher pH values than the soils in which *Atriplex confertifolia* grew. This agrees with the findings of Flowers and Evans (1965). In our study *Atriplex confertifolia* (Fig. 4) and *Sarcobatus vermiculatus* were most frequent in soils with pH values around 8.5, with *Atriplex confertifolia* exhibiting higher frequencies at slightly higher pH values. The hydrogen ion concentration preference values (Table 5) for these two species were 8.46 for *Sarcobatus vermiculatus* and 8.51 for *Atriplex confertifolia*.

The response of the plant growth forms to

the hydrogen ion concentration gradient were, in most cases, dissimilar with respect to their responses to total soluble salts and soil moisture and tended to indicate an independent effect of pH upon the distribution of the plant species. Ungar, Hogan, and McClelland (1969), on the basis of results from their study of saline areas near Lincoln, Nebraska, stated that hydrogen ion concentration had little or nothing to do with plant distribution, but, as shown by the evidence from this study, hydrogen ion concentration was a factor in the distribution of plant species around the Goshen salt playa. This conclusion is in agreement with the findings of Fireman and Hayward (1952).

Due to the time of year that soil samples were taken, it is felt that some of the data presented in this study may be somewhat misleading. Specifically, the data pertaining to annual habit and gradient correlations may be incorrect. This is because the plant *sBromus tectorum*, *Lepidium perfoliatum*, *Camelina microcarpa*, and *Descurainia sophia* (all spring annuals) had completed their life cycles before the time soil samples were taken. These species germinate and complete their life cycle in the spring when there exist more favorable moisture conditions in their habitats. During this time of year, the excess moisture probably leaches the soil salts downward and out of reach of the roots of these spring annuals. As the soil dries during early summer the salts are returned to the surface by the wicking action described by Hansen and Weber (1975). Thus, although the annuals did occur on some saline sites, the sites probably were far less saline while the annuals were alive and growing.

LITERATURE CITED

- AL-JIBURY, L. K. 1972. Salt tolerance of some desert shrubs in relation to their distribution in the southwestern desert of North America. Unpublished Ph.D. dissertation, Arizona State University, Tempe.
- ANDERSON, O. 1964. The phytosociology of dry lime prairies of Wisconsin. Unpublished Ph.D. dissertation, University of Wisconsin, Madison.
- BARBOUR, M. G. 1970. Is any angiosperm an obligate halophyte? *Am. Midl. Nat.* 84:105-120.
- BEADLE, N. C. W., R. D. B. WALLEY, AND J. B. GIBSON. 1957. Studies in halophytes. II. Analytic data on the mineral constituents of three species of *Atri-*

- plex* and their accompanying soils in Australia. *Ecology* 38(2):340-34.
- BLOSS, D. A. 1974. Some aspects of vegetation response to moisture gradient on an ephemeral stream in central Arizona. Unpublished M.S. thesis, Brigham Young University, Provo, Utah.
- BUCKMAN, H. O., AND N. C. BRADY. 1969. The nature and properties of soils. Macmillan Co., London.
- CHAPMAN, V. J. 1966. Vegetation and salinity. In: Salinity and aridity: new approaches to old problems. Hugo Boyko (ed.). Dr. W. Junk Publishers, The Hague.
- CURTIS, J. T. 1959. The vegetation of Wisconsin. University of Wisconsin Press, Madison, 657 p.
- DAUBENMIRE, R. E. 1959. Plants and environment. John Wiley & Co., New York.
- DICK, A. V. 1971. Tuscarora Meadow: a plant community study. Unpublished M.S. thesis, University of Utah, Salt Lake City.
- DREGENE, H. E. 1963. Soils of the arid west. In: Aridity and man: the challenge of the arid lands in the United States. C. Hodge and P. C. Duisberg (eds.). Am. Assoc. Adv. Sci., Washington, D.C. Publ. No. 74:215-238.
- FAUTIN, R. W. 1946. Northern desert shrub biome in western Utah. *Ecol. Mono.* 16:251-310.
- FIREMAN, M., AND H. E. HAYWARD. 1952. Indicator significance of some shrubs in the Escalante Desert, Utah. *Bot. Gaz.* 114:145-155.
- FLOWERS, S., AND F. EVANS. 1965. The flora and fauna of the Great Salt Lake region, Utah. In: Salinity and aridity: new approaches to old problems. Hugo Boyko (ed.). Dr. W. Junk Publishers, The Hague.
- GATES, D. M., L. A. STODDART, AND C. W. COOK. 1956. Soil as a factor influencing plant distribution on salt deserts of Utah. *Ecol. Mono.* 26:155-175.
- GOODMAN, P. J. 1973. Physiological and ecotypic adaptations of plants to salt desert conditions in Utah. *Jour. Ecol.* 61:473-494.
- GOODMAN, P. J., AND M. M. CALDWELL. 1971. Shrub ecotypes in a salt desert. *Nature*, London 232:571-572.
- HALL, H. H. 1971. Ecology of a sub-alpine meadow of the Aquarius Plateau, Garfield and Wayne counties, Utah. Unpublished Ph.D. dissertation, University of Utah, Salt Lake City.
- HANSEN, D. J. 1974. Aspects of salt tolerance of *Salicornia pacifica* Standl. var. *utahensis* (Tides.) Munz. Unpublished M.S. thesis, Brigham Young University, Provo, Utah.
- HANSEN, D. J., AND D. J. WEBER. 1975. Environmental factors in relation to the salt content of *Salicornia pacifica* var. *utahensis*. *Great Basin Nat.* 35:86-96.
- HARRIS, F. S. 1920. Soil alkali, its origin, nature and treatment. John Wiley & Sons, Inc., New York.
- KRAMER, P. J. 1956. Roots as absorbing organs. *Encycl. Plant Physiol.* 3:118-214.
- LAMBERT, C. B. 1940. The distribution of plant types in the Escalante Desert of Utah with relation to soil conditions. Unpublished M.S. thesis, Brigham Young University, Provo, Utah.
- LEVINS, R. 1966. The strategy of model building in ecology. *Am. Sci.* 54:421-431.
- MACARTHUR, R. H. 1972. Geographical ecology: patterns in the distribution of species. Harper and Row, New York. 251 p.
- MAGISTAD, O. C. 1945. Plant growth relations on saline and alkali soils. *Bot. rev.* 11:181-230.
- OLSEN, C. 1924. Studies in the hydrogen ion concentration of the soil and its significance to the vegetation, especially to the natural distribution of plants. *J. Ecol.* 12:139-142.
- PHILLIPS, E. A. 1959. Methods of vegetation study. Holt, Rinehart and Winston, Inc. New York. 107 p.
- QUIGLEY, B. H. 1956. The interrelation and interaction of *Allenrolfea occidentalis* and its edaphic environment. Unpublished M.S. thesis, Brigham Young University, Provo, Utah.
- RAHEJA, P. C. 1966. Aridity and salinity (a survey of soils and land use.) In: Salinity and aridity: new approaches to old problems. Hugo Boyko (ed.). Dr. W. Junk Publishers, The Hague.
- SNEDECOR, G. W., AND W. G. COCHRAN. 1968. Statistical methods. Iowa State University Press, Ames, Iowa. 593 p.
- UNGAR, I. A. 1966. Salt tolerance of plants growing in saline areas of Kansas and Oklahoma. *Ecol.* 47:154-155.
- UNGAR, I. A., W. HOGAN, AND M. MCCLELLAND. 1969. Plant communities of saline soils at Lincoln, Nebraska. *Am. Midl. Nat.* 82:564-577.
- WAISEL, Y. 1972. Biology of halophytes. Academic Press, New York.